

## THE BIOLOGY OF A BROODING SEASTAR, *LEPTASTERIAS TENERA*, IN BLOCK ISLAND SOUND

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### ABSTRACT

*Leptasterias tenera* (Stimpson) was sampled from a muddy habitat, 28-37 m deep, dominated by tubicolous amphipods. The seastars were seldom aggregated and had mean densities of 3-8 individuals per m<sup>2</sup>. *L. tenera* is holophagous, feeding primarily on small crustaceans which they capture with the pedicellariae and tube feet. Approximately half of the branched testes in mature males are degenerated or absent, but females usually have 10 lobate ovaries. Females initially brood embryos in their pyloric stomach and hold them externally during the latter half of the brooding period. The embryos are attached in cohesive masses by their elongate brachiolar appendages. *L. tenera* is slow-growing and iteroparous. The gonad and digestive caecum organ indices of *L. tenera* are not in phase with each other. Caecum index values indicate that females neither store more nutrient, nor utilize more reserves during the brooding period than males. Sexually mature males appear to have a higher rate of mortality than females. Thus, additional parameters must be examined to determine whether there is an energetic cost attributable to brooding adaptations in *Leptasterias*. It is possible that brooding specializations, small size, and slow growth rates typical for *Leptasterias* species are "cold adaptations" (*sensu* Clarke, 1980) rather than a coadaptive consequence of competition as suggested by Menge (1975) for *Leptasterias hexactis*.

### INTRODUCTION

The genus *Leptasterias* Verrill contains over 30 species of generally small, 5 or 6 armed seastars which brood their young. The genus is restricted to the North Atlantic, North Pacific and the Arctic Oceans (Fisher, 1930; Djakonov, 1938). The life histories of several intertidal *Leptasterias* species have been examined (Chia, 1966, 1968a, b, 1969; Smith, 1971; Menge, 1972, 1974, 1975; O'Brien, 1976). This report on *Leptasterias tenera* (Stimpson) is the first ecological study of a subtidal species, although its reproductive cycle has been discussed in detail (Worley, *et al.*, 1977).

*L. tenera* is found along the eastern coast of North America from southwest Greenland to Cape Hatteras, North Carolina at depths from 18 to 230 m (Mortensen, 1927, 1932; Gray, *et al.*, 1968; Worley, *et al.*, 1977; Franz, *et al.*, 1981). The population of *L. tenera* studied occurred at depths of 28-37 m off the western side of Block Island. This is an area of muddy, fine sand with extensive patches dominated by "carpets" of tube-building ampeliscid amphipods and occasional mounds of bivalve shells. This subtidal, soft-bottom habitat of *L. tenera* contrasts markedly with the rocky environments of those intertidal *Leptasterias* species previously studied. Certain specializations of *L. tenera*, discussed below, include their

holophagous feeding habits and their alternation of internal and external brooding during the initial and final segments of the brooding period.

### MATERIALS AND METHODS

From 1971 to 1972 *L. tenera* was dredged monthly in Block Island Sound, Rhode Island, U. S. A., between 41° 11.4' N, 71° 38.3' W (Station C) and 41° 12.1' N, 71° 36.2' W (Station D). Specimens for dissection were transferred immediately to the laboratory in aerated, refrigerated water and others were preserved in seawater formalin for analysis of stomach contents. Small specimens were collected by washing dredge or grab haul sediments on 0.85 mm or 1.0 mm sieves.

All seastars were measured to determine a radius (R), the distance from the center of the disc to the tip of the longest arm. Organ indices, ratios between the weight of an organ system and the weight of an organism (Giese and Pearse, 1974), were used to describe quantitatively the dynamics of the reproductive cycle. For organ index measurements, whole specimens, freshly dissected gonads, and digestive caeca were drained and wet weighed. Organ indices were determined for 5 males and 5 females each month.

The density and dispersion of *L. tenera* were estimated from bottom photographs, each encompassing a 1.39 m<sup>2</sup> quadrat. Photographs were taken randomly in August 1970 and December 1971 using an automatically triggered benthic camera system towed across the study area. Dispersion was analyzed using the nearest-neighbor method of Clark and Evans (1954) as outlined in Poole (1974), a method which has been applied to the analysis of aerial photographs by Miller and Stephen (1966). The average distance between individuals and their nearest neighbors ( $\bar{r}$ ), determined from the photographs, was compared with the expected distance ( $E_r$ ) assuming a random distribution. The ratio (R) between observed ( $\bar{r}$ ) and expected ( $E_r$ ) values is equal to 1.0 if the seastars are randomly dispersed. Aggregated populations have values of R between 0 and 1.0, and regularly dispersed populations have values between 1.0 and 2.1496. The significance of the deviation from the expected value of R is determined using a standardized variate of the normal curve,  $Z = \bar{r} - E_r / SE(\bar{r})$ , where  $SE(\bar{r})$  is the standard error of the mean observed nearest-neighbor distance (Poole, 1974).

Feeding periodicity and prey diversity were determined by analysis of stomach contents. The prey capture behavior of *L. tenera* from Cape Cod Bay was observed in running seawater aquaria at the Woods Hole Oceanographic Institution between March and June, 1974.

### RESULTS

#### *Density and dispersion*

Dredging and photography showed that *L. tenera* was the most conspicuous and numerous epifaunal, predatory macroinvertebrate in the Block Island Sound Basin. Other predators such as the crab *Cancer borealis* Stimpson and the seastars *Asterias forbesi* (Desor) and *Asterias vulgaris* Verrill were present. The density of *L. tenera* in the study area ranged from 0 to 12 individuals per m<sup>2</sup>, with means of 3-8 per m<sup>2</sup> (Table I). Of the 20 bottom photographs analyzed to determine dispersion (Table II), 15 indicated patterns which did not differ significantly from random dispersion. Five photographs indicated moderate to small, though statistically significant, deviations from randomness, toward aggregated patterns.

TABLE I

*Density of Leptasterias tenera in Block Island Sound based on the analysis of random underwater photographs.*

	Station C 9 XII 1971	Station C 5 VIII 1970	Station D 9 XII 1971
No. photographs	8	5	12
$\bar{x}/m^2$	4.80	7.97	3.32
Range/ $m^2$	1.45-10.14	5.07-11.59	0-7.97

### Feeding

In laboratory aquaria *L. tenera* behaved as a "sit and wait" predator. Individuals remained stationary for hours and captured small crustaceans that contacted their arms. Prey were grasped both by pedicellariae and tube feet on a seastar's arm and transferred to the mouth by flexing the arm under the disc (Fig. 1). Laboratory and field observations showed that when particularly large food items were ingested only the portion of an object within the pyloric stomach was digested. Generally, only one or two items were found in the stomachs of actively feeding *L. tenera*.

TABLE II

*Nearest-neighbor analysis of the spatial distribution of Leptasterias tenera in Block Island Sound based on random underwater photographs. Calculation of the index of dispersion and statistical significance is described in the text.*

STATION C 5 VIII 1970			
Photograph number	R	Z	Significance
1	1.036	0.294	NS
2	0.892	-1.000	NS
3	0.589	-2.954	0.01
4	0.693	-2.613	0.01
5	0.545	-5.000	0.01
STATION C 9 XII 1971			
6	0.820	-1.395	NS
7	0.657	-2.064	0.05
8	1.006	0.045	NS
9	0.865	-1.364	NS
10	1.095	0.447	NS
11	0.962	-0.272	NS
12	1.174	0.669	NS
13	0.669	-2.159	0.05
STATION D 9 XII 1971			
14	1.036	0.321	NS
15	0.868	-0.790	NS
16	0.948	-0.464	NS
17	0.994	-0.045	NS
18	1.101	0.061	NS
19	0.914	-0.614	NS
20	0.864	-1.053	NS

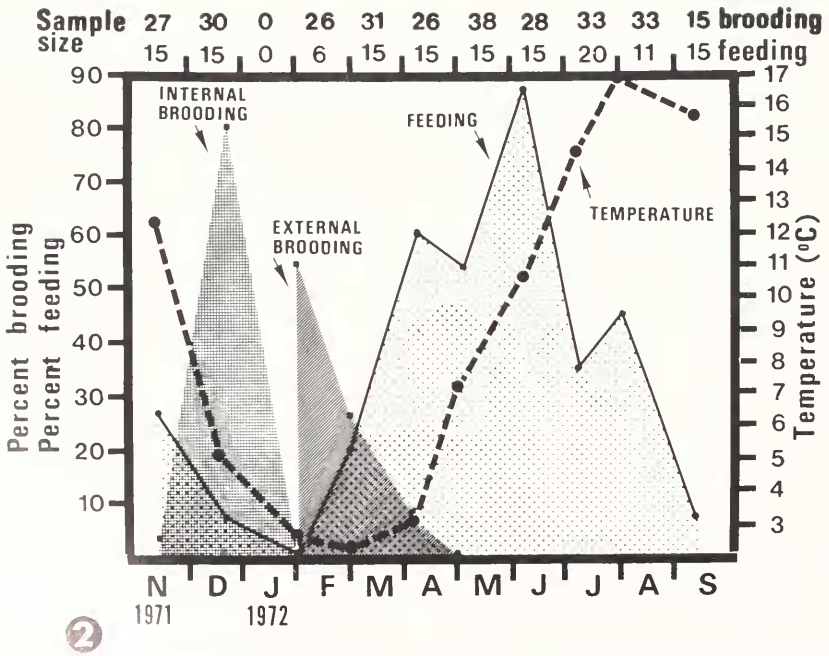


FIGURE 1. *Leptasterias tenera* feeding on an amphipod in a laboratory aquarium. The prey was captured with pedicellariae on the dorsal surface of the bent arm, transferred to the tube feet, relayed proximally along the arm, and brought to the mouth by arm flexure.

FIGURE 2. A composite graph showing the percentage of *Leptasterias tenera* with prey in their stomachs (internal) and in an



taken in field collections although up to five amphipods were found in the stomach of a single specimen.

The percentage of feeding *L. tenera* in the population varied seasonally (Fig. 2). Feeding peaked in June, declined during the summer, and was lowest in winter. While feeding rates approached zero in February, our sample size in this month was too small to rule out the possibility that *L. tenera* feeds during this period. In a supplementary sample collected on 29 February 1972, 5 of 25 males (20%) contained partially digested amphipod remains while 20 males (80%) had empty stomachs. Of the 5 females, 3 had empty stomachs.

The benthic community at the sampling sites in Block Island Sound was dominated by amphipods, with *Ampelisca agassizi* (Judd) making up 90% of all individuals. In spite of high amphipod numbers, the community was rich in polychaete species (25 of a total of 41), only a few of which were abundant (Table III). Stomach content analysis of 177 *L. tenera* collected between November 1971 and December 1972 indicated that *A. agassizi* made up 95% of their prey items (Table IV). Despite the diversity and numbers of polychaetes available, few were found in seastar stomachs.

In northeastern Block Island Sound near Fishers Island, the bottom sediments were coarse sand and gravel which supported a high diversity of epibenthic species (Abbott, 1971) but lacked the carpets of ampeliscid amphipod tubes which occurred elsewhere in Block Island Sound. Here *L. tenera* fed on a greater variety of prey species, and relatively few amphipods (Table IV).

### *Seasonality and reproduction*

Female *L. tenera* in Block Island Sound spawned and began to brood in November and continued to brood through March (Fig. 2). The few seastars still holding young at the beginning of April were brooding slow-developing, abortive embryos. Thus, the period of brood protection encompassed approximately four months, although each female did not necessarily brood over that entire period.

The gonad index of *L. tenera* decreased abruptly during winter spawning (from November to December) then gradually increased beginning in June the following year (Fig. 3). The pyloric caecum index reached a maximum value during the extensive spring-summer feeding period with the highest monthly mean in June. It dropped during the period of maximum gonadal growth (as the feeding rate fell), showed a significant decline by the beginning of August, and slowly decreased during the winter. The general trends in organ indices were similar for males and females, although the male gonad index increased more precipitously and reached a significantly greater value than the ovarian index.

In March, free-living juvenile *L. tenera* appeared in the benthic samples in Block Island Sound (Fig. 4), indicating that the brooding period was ending. There was some evidence of regular winter brooding for other populations of *L. tenera*. We examined specimens of *L. tenera* from the Cape Cod Bay Faunal Survey (Young, *et al.*, 1971). The gonad lengths measured as a percentage of total arm length for seastars from samples taken over a two year period showed a sharp decrease in gonadal size by December 1967 and January 1968, suggesting that

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external brood chamber, and the bottom water temperature. The number of specimens examined in the monthly samples for feeding and reproduction is indicated at the top of the graph. The samples were collected (1971) 1 October, 12 November, 21 December, (1972) 1 February, 29 February, 7 April, 2 May, 8 June, 6 July, 2 August, and 11 September.

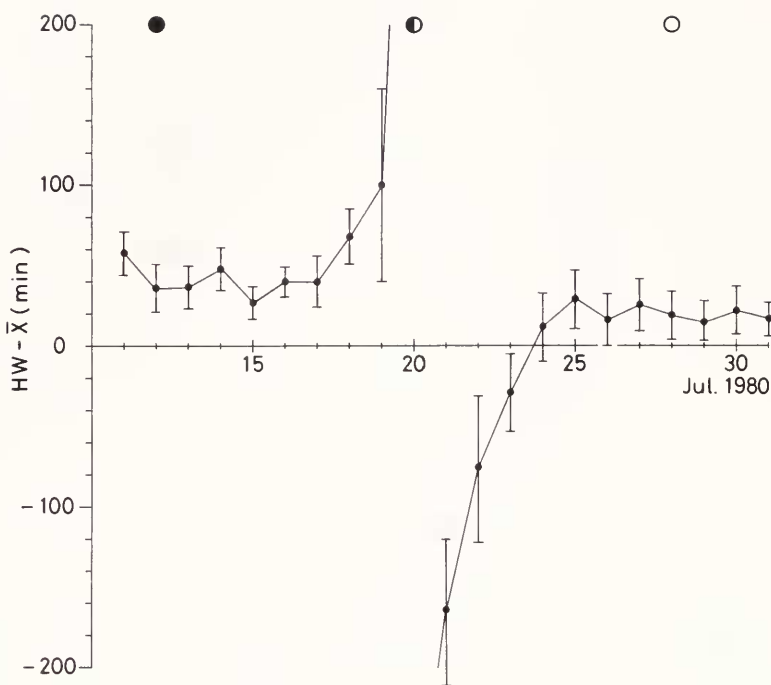


FIGURE 6(A): Correlation between the timing of larval release by the Kasaoka population and the time of high water, 11–31 July 1980. The estimated time from the average peak of the larval release activity ( $\bar{X}$ ) to the time of high water (HW) is plotted. HW indicates the time of high water with which larval release coincided. Temporal variation in larval release activity is indicated by standard deviation. Though a nighttime period virtually extended two days, larval release from 24:00 till dawn is included on the date preceding the actual date.

of the Izu Peninsula. Thus, high water in Kasaoka occurs about noon and midnight at the spring tides and around sunrise and sunset at the neap tides.

In this study site, the river flat emerged at the low water periods, when the river became 5–6 m wider and about 5 cm deeper. The entire estuarine flat was submerged during the high water periods, when the maximum depth of the middle part of the river was recorded at night to be 2.5 m in July and 2.2 m in September. Although few measurements were made of the daytime high water, the tide table indicated that the water level during summer was always lower at the daytime high water than at the nighttime high water, and that the difference between them was 30–50 cm at the spring tides. The water level at the neap tides was recorded at 1.5–1.8 m in the morning and evening high-water periods. Though some difference could be seen in the water level at the high water periods according to the season and lunar phase, it had relatively little influence on the period of emersion and submersion of the mud flat (Fig. 3).

Salinity changed remarkably with ebb and flow of the tides. Also, at high water periods, a considerable difference in salinity was often recorded between water edge or surface and a place where the water was somewhat deeper. The periodic fluctuations in salinity showed a similar pattern in spring and neap tides (Fig. 4).

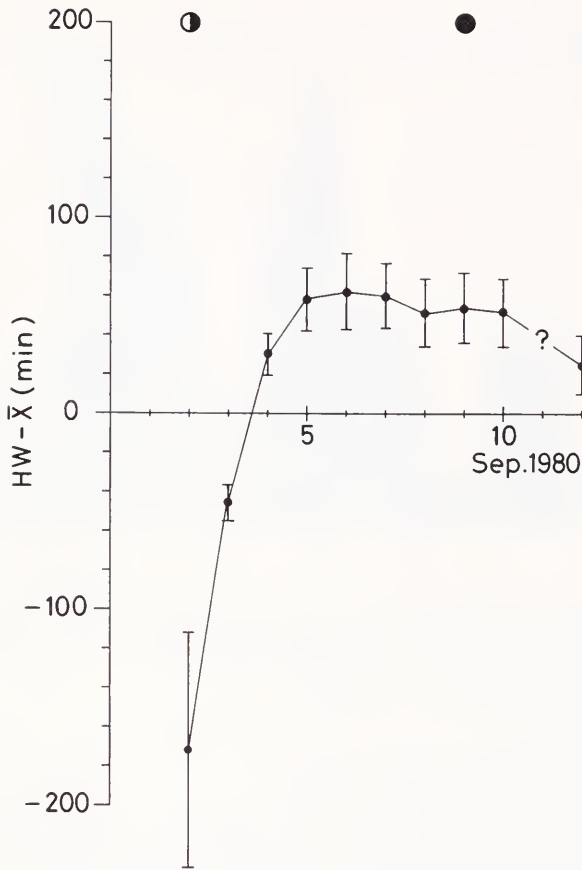


FIGURE 6(B): Correlation between the timing of larval release by the Kasaoka population and the time of high water, 1-12 September 1980. The value for  $HW - \bar{X}$  was calculated by the same method shown in Figure 6A.

#### *Semilunar rhythm of larval release at Kasaoka*

The time of day of larval release at Kasaoka is shown in Figure 5. It is evident that the time of day of larval release did not coincide with a lunar day cycle, but with a local tidal cycle. Larvae were released only at night, suggesting that the solar day cycle suppressed daytime larval release in all cases. In addition, larval release activity revealed a combined pattern of 24 h solar day and 24.8 h unimodal tidal components, corresponding to the phase relationship between a solar day cycle and 12.4 h tidal cycle. The solar day component appeared when high water came about sunset and sunrise, and the tidal component appeared at different times.

When the larval release activity revealed a strong correlation with nighttime high water, the average activity peak ( $\bar{X}$ ) was a little before the high water (HW) (Fig. 6A, B). The estimated time from  $\bar{X}$  to HW then differed somewhat in tidal cycles during the night: 42 min from 11 to 17 July, 17 min from 24 to 31 July, and 49 min from 4 to 12 September, respectively on the average. The average peak

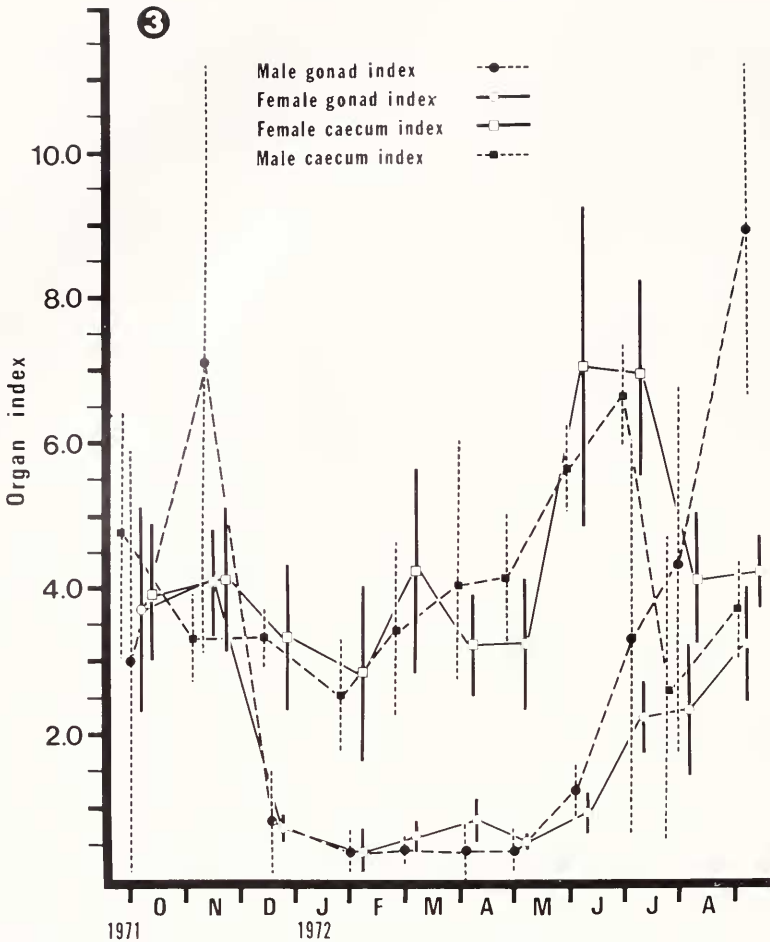


FIGURE 3. Organ indices for *Leptasterias tenera* in Block Island Sound. The mean and 95% confidence intervals are shown for the data from 5 males and 5 females in each sample. Sampling dates as in Figure 2.

that the young seastars showed a 1:1 sex ratio, but that the sex ratio for individuals of breeding size differed significantly from unity, favoring females.

#### *Fecundity and gonadal dimorphism*

*L. tenera* examined typically had two gonads in each arm. The ripe ovaries were small, lobate, and concentrated at the base of the arm, and mature testes were branched and some (by folding) exceeded the arm in length (Worley, *et al.*, 1977). The contrasting size of the gonads in males and females of different sizes is shown in Figure 8. The length of the ovaries was directly proportional to the size of the seastar (Fig. 8). The number of oocytes was also a direct function of the size of the female (Worley, *et al.*, 1977).

Coefficients of determination ( $r^2$ ) calculated from the sets of data for males and females show that 91% of the variability of ovary length, but only 18% of the variability of testis length, is explained by the size of the seastar (Fig. 8). Thus,



for male and female seastars of identical size, there is less variability expected in ovary length than in the length of the testes. In addition, the testes were often degenerated or even absent in some arms. During the period of maximum gonadal development, an average of only half of the testes in mature males were fully developed. Of the rest, 25% were drastically less than the maximum size and darkly pigmented, and some rays lacked one or both testes ( $n = 29$  males, from combined samples collected 12 November 1971 and 11 September 1972). Female *L. tenera* occasionally had less than 10 ovaries but such morphological irregularities were considerably rarer than in males (one individual with only 8 ovaries was found among 330 dissected females).

## DISCUSSION

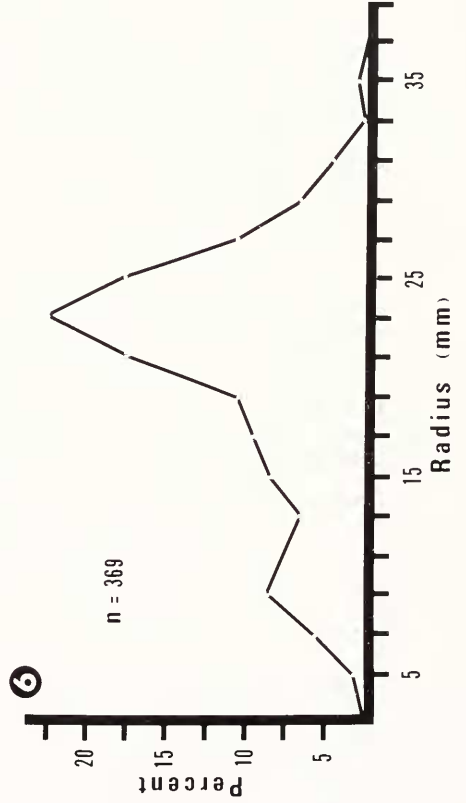
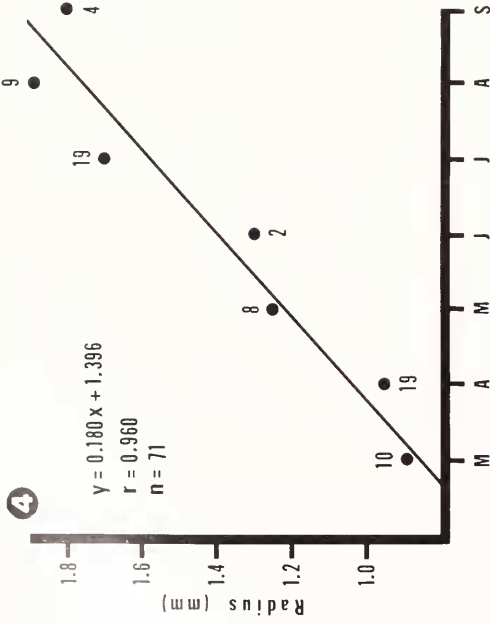
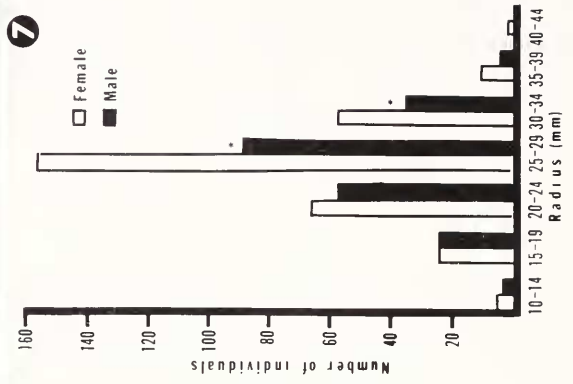
### Feeding

The feeding habits of *L. tenera* differ from those of the intertidal species of the Pacific Coast of the United States including *L. aequalis*, *L. hexactis*, and *L. pusilla* (Smith, 1971; Menge, 1972). The habit of prey capture with pedicellariae, and internal digestion rather than stomach eversion, restricts the prey of *L. tenera* to small organisms (primarily small crustaceans and mollusks). It is interesting that *L. littoralis* (Stimpson), a 5 armed, northwestern Atlantic species, has a diet similar to *L. tenera* and ingests small prey using its tube feet for prey capture (O'Brien, 1976). The only other seastars known to capture prey with pedicellariae are *Stylasterias forreri* (de Loriol) and possibly *Labidiaster annulatus* Sladen (Robilliard, 1971; Chia and Amerongen, 1975; Dearborn, 1977). Unlike *Stylasterias*, *Leptasterias* does not have greatly modified pedicellariae (Fisher, 1930). This supports Robilliard's (1971) contention that pedicellaria capture is a modification of a generalized asteroid behavior pattern that is not confined to morphologically specialized forms.

*L. tenera*, as well as *L. hexactis*, *L. pusilla*, and *L. littoralis*, exhibits an annual unimodal feeding pattern (Smith, 1971; Niesen, 1973; O'Brien, 1976). The incidence of feeding individuals in the population peaks in the late spring to early summer and declines before the occurrence of the annual maximum bottom temperature (Fig. 2).

Our data suggest that, in central Block Island Sound, *L. tenera* occur more or less randomly within a prey patch of *Ampelisca* tubes. In bottom photographs much of the area covered by amphipod tubes appears homogeneous, although some aggregations of seastars occur within this habitat (Table II). However, coarse-scale patchiness of the benthic habitat is related to areas of shelly bottoms, notably shells of *Arctica islandica*, which appear as windrows in bottom photographs, and which lack both amphipod tubes and *Leptasterias*.

Amphipods dominate the macrobenthos in the central basin of Block Island Sound (Table III) and are also the dominant taxa in the diet of *L. tenera* (Table IV). In Cape Cod Bay, *L. tenera* feeds extensively on caprellid amphipods (O'Brien, pers. comm.). However, in northern Block Island Sound, amphipods are less abundant and the diversity of prey taxa in the diet of *L. tenera* increases, probably in correlation with the composition of the benthic community (Table IV). Although amphipods are the major component of the diet in central Block Island Sound, there is no evidence from this study that *L. tenera* feeds preferentially on amphipods. However, O'Brien (1976) found that in simple choice experiments, amphipods were the preferred prey of *L. littoralis*. There is a possibility that *L. tenera* may also prefer amphipods, but experimental evidence is needed.



Polychaetes do not appear to make a significant contribution to the diet of *L. tenera* even though the central basin of Block Island Sound supports a relatively diverse worm fauna (Table III). We do not know whether *L. tenera* avoids polychaetes or is simply unsuccessful at capturing them. However, other holophagous asteroids, notably species of *Astropecten*, discriminate against polychaetes (Christensen, 1970; Ribi, *et al.*, 1977; Franz and Worley, pers. comm.).

Other *Leptasterias* species also have circumscribed diets and a seeming tendency to prey on locally abundant resources. For example, subtidal populations of *L. hexactis* in Puget Sound, Washington, feed almost exclusively on the holothuroid *Cucumaria lubrica* Clark, and in kelp communities feed on the gastropod mollusk *Lacuna* spp. (Mauzey, *et al.*, 1968; Niesen, 1973). Feder and Jewett (1980) report that in the southeastern Bering Sea, *Leptasterias polaris acervata* (Stimpson) feeds solely on the cockle, *Clinoecardium ciliatum* (Fabricius). However, it is noteworthy that sympatric *Leptasterias* species may show different feeding habits. *L. pusilla*, in California tide pools, feeds almost entirely on the small snail *Barleeia acuta* (Carpenter), while *L. aequalis* in the same habitat consumes gastropods, mussels, limpets, polychaetes, and even small seastars and detritus (Smith, 1971).

#### *Modes of brooding in Leptasterias species*

Three modes of brooding have been described in previous studies of *Leptasterias*. In the first type, exhibited by *L. ochotensis similispinis* (Clark), the eggs adhere to the substratum beneath the female (Kubo, 1951). In the second type (*e.g.* in *L. aequalis* (Stimpson), *L. alaskensis* (Verrill), *L. hexactis* (Stimpson), *L. muelleri* (Sars), and *L. pusilla* Fisher) the female holds the eggs and embryos in a "brood chamber" beneath her arched disc and arms (Sars, 1846; Fisher, 1930). In the third mode, that of *L. groenlandica* (Lütken), the female holds both the eggs and embryos in the cardiac portion of her stomach until the juveniles emerge (Lieberkind, 1920).

*L. tenera* shows characteristics of both the second and third modes described above. Embryos of *L. tenera* (at least until the late gastrula stage) are held in the pyloric chamber of the mother's stomach, and brachiolariae and later stages reside in a brood chamber beneath the disc of the female before they emerge and disperse. The behavioral mechanism involved in embryo transfer was not observed, but it might resemble that described by Chia (1966) for *L. hexactis*.

Our examination of the literature shows that *Leptasterias* species with external and internal brooding have different types of embryos. Those species which brood internally have an amorphous membranaceous nucleus of unknown composition to which the embryos attach (Fig. 5). The embryos of *L. groenlandica* are attached to such a central mass by a long, thin preoral lobe that is tipped with minute brachiolar arms (Fisher, 1930), as are the embryos of *L. tenera*. It is possible that

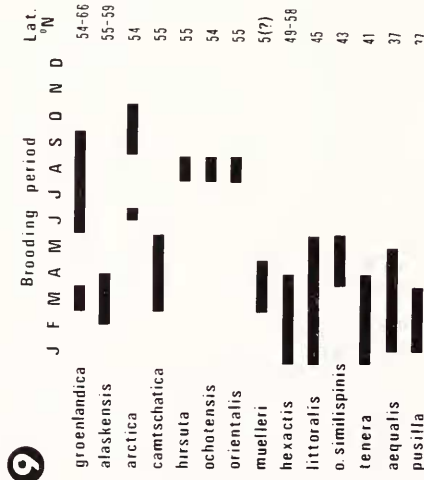
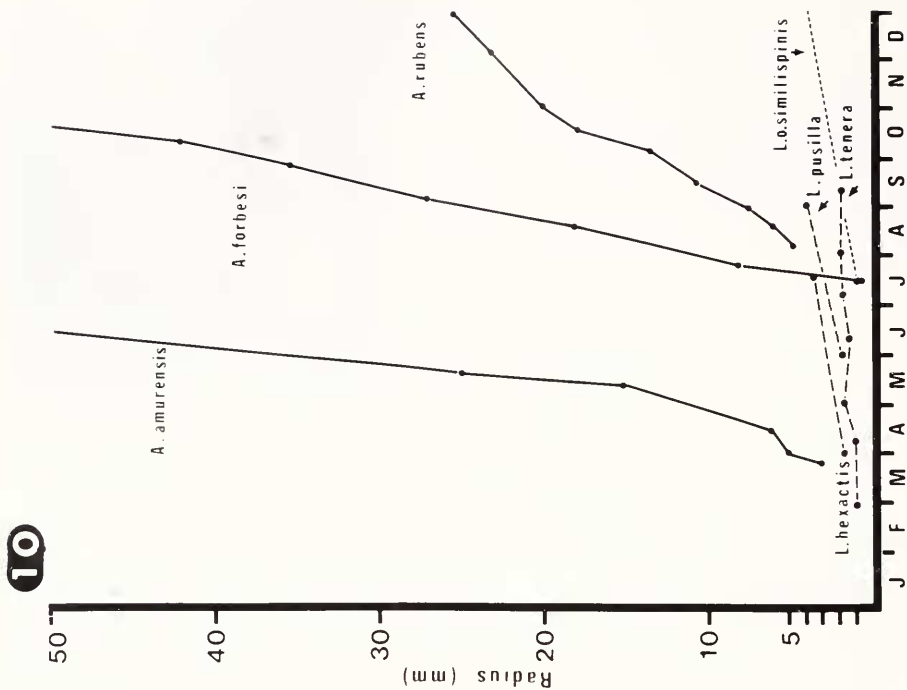
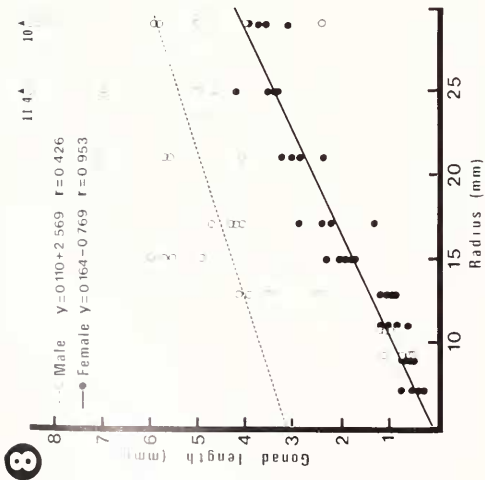
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FIGURE 4. A plot of the mean size of juvenile *Leptasterias tenera* from semimonthly collections in Block Island Sound, October 1971 to May 1972. Sample size is indicated by the number near each datum point.

FIGURE 5. A cluster of *Leptasterias tenera* embryos photographed on 1 February 1972. At this stage the brachiolar appendages (arrows) which connect the embryos to a central membranaceous mass are capable of moving, as are the tube feet of the developing seastars. Scale is 1 mm.

FIGURE 6. Size-frequency distribution of adult *Leptasterias tenera* dredged between Stations C and D, west of Block Island, 9 July 1974.

FIGURE 7. Size-frequency histograms of male and female *Leptasterias tenera* collected in Block Island Sound from October 1971 to September 1972. Each size class was tested for agreement with a 1:1 sex ratio, and size classes differing significantly from unity (Chi-squared test,  $P < 0.05$ ) are marked with an asterisk. No males were sampled in the 40-44 mm size group.



the central mass is composed of fertilization membranes which coadhere after the embryos hatch in the mother's stomach.

The embryos of externally brooding species have compact preoral lobes and do not develop bonds to each other or to the brood chamber (e.g. Gordon, 1929; Chia, 1968a). As a test of this inferred correlation between the mode of brooding and the morphology of the embryos we predict that *L. arctica* (Murdoch), which Fisher (1930) illustrated with a nucleus of embryo attachment, broods embryos within its stomach.

Although there may be phylogenetic affinities between species with similar brooding types (e.g., all known purely external brooders are in the subgenus *Hexasterias*, the 6 armed *Leptasterias*), it is possible that brooding specializations have evolved in response to the specific environmental pressures experienced by each species. *L. ochotensis similispinis*, for example, spawns on hard substrates. Its egg masses are sessile and the female remains stationary during brooding (Kano, *et al.*, 1974). In contrast, internal brooding may permit greater freedom of movement, an adaptation especially important for species such as *L. tenera* living on soft or unstable substrates. A centrally connected embryo mass could facilitate retention of a brood by a moving female. On the other hand, for species occupying hard substrates in high energy environments, unconnected embryos could be advantageous since less than the whole clutch need be lost if a brooding female were dislodged by wave action. Finally, external brooding may raise the limits of brood size for some species, since the clutch volume of internal brooders must be limited by the capacity of the stomach to accommodate and maintain viable ova.

#### Cycles of reproduction

*L. tenera* in Block Island Sound, Cape Cod Bay, and Massachusetts Bay spawns during the winter (Fewkes, 1888; this paper). This reproductive pattern may be related to the natural decrease in prey abundance during cold weather (Chia, 1968b), or to the seasonal inactivity of predators on seastars and their embryos. The spawning of *L. hexactis* and *L. pusilla* during the winter could help provide the newly released young with an optimal supply of food (Chia, 1968b; Smith, 1971; Menge, 1975). However, apart from Niesen's (1973) observations that young *L. hexactis* feed on newly settled *Spirorbis* species, there is no information on the diet of juvenile *Leptasterias* species in the field.

The literature indicates that many *Leptasterias* species brood during the winter. Exceptions are, for example, *L. ochotensis similispinis* in Japan which broods during April-May, and the brooding specimens of high latitude species collected

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FIGURE 8. Gonad length as a function of body size (radius) of male and female *Leptasterias tenera*. Each point represents the mean length of the gonads in one seastar.

FIGURE 9. Brooding periods of *Leptasterias* species arrayed according to latitude, showing that the brooding period is shorter in a low than in high latitudes. Data on the duration of brooding periods are incomplete for species north of 50°N latitude. References: *L. groenlandica*, Djakonov, 1938; Fisher, 1930. *L. camtschatica*, Djakonov, 1938. *L. hirsuta*, Djakonov, 1938. *L. ochotensis*, Djakonov, 1938. *L. orientalis*, Djakonov, 1938. *L. muelleri*, Sars, 1846; Mortensen, 1927. *L. hexactis*, Osterud, 1918; Menge, 1974. *L. littoralis*, Verrill, 1895. *L. ochotensis similispinis*, Kubo, 1951. *L. tenera*, this report. *L. aequalis*, Fisher, 1930; Hewatt, 1938; Smith, 1971.

FIGURE 10. Growth rates of newly settled *Leptasterias* and co-occurring forcipulate seastars. References: *L. hexactis*, Osterud, 1918. *L. pusilla*, Smith, 1971. *L. ochotensis similispinis*, Kano, *et al.*, 1974. *L. tenera*, this report. *Asterias amurensis*, Ino, *et al.*, 1955; Hatanaka and Kosaka, 1959. *A. forbesi*, Mead, 1900. *A. rubens*, Barnes and Powell, 1951. The growth rate of *L. ochotensis similispinis* is based on an extrapolation between measurements of the mean size of individuals in the first growth season and of the first year class.



during the summer months (often the only season when the northernmost taxa are accessible) (Fig. 9). The relationship between latitude and brooding period in the genus as a whole (Fig. 9) seems to fit the pattern expected for a high latitude species, with a brief spawning period during low temperature seasons in warm climates and more extended spawnings in cold climates (Orton, 1920). As more data accumulate on the reproductive periodicity of *Leptasterias* species it may be possible to determine whether the distribution of the genus is limited to regions with water temperatures required for successful reproduction. For certain species temperature can clearly be a critical factor in reproduction, and O'Brien (1976) has indicated that falling temperatures may trigger spawning in *L. littoralis*. Although brooding does appear to be correlated with temperature, the ultimate selective factor for the brooding period is not known.

Figure 3 shows that the caecum and gonad index cycles of *L. tenera* are out of phase. This is not unexpected, for as Harrold and Pearse (1980) point out, although the inverse relationship between the gonadal and caecum indices has often been emphasized, not all seastars show a strict inverse pattern. The change in the size of asteroid caeca is probably related to multiple functions of the organs (digestion and mobilization, distribution, and storage of nutrients) and is strongly influenced by temperature sensitive rate functions and the availability of food, rather than being primarily determined by reproductive effort (Lowe and Dearborn, 1979; Van der Plas, *et al.*, 1980; Oudejans, *et al.*, 1980; Harrold and Pearse, 1980).

The caecum indices of male and female *L. tenera* are similar and show a slight (not statistically significant) decrease during the brooding period. The male gonad index, however, rises more abruptly and reaches a higher value than the gonad index of the females (Fig. 3). Some populations of *L. hexactis* and *L. pusilla* have organ index patterns much like *L. tenera* (Smith, 1971; Niesen, 1973). For example, *L. hexactis* in Oregon may show no detectable decrease in the caecum index during brooding (Niesen, 1973). These observations appear to contradict Menge's (1975) hypothesis that brooding female *L. hexactis* must invest more energy than males do in the storage of nutrients and that their caecum index should drop more sharply than the male index during the brooding period because the brooding females cannot feed and recoup nutrient losses.

### *Growth and population dynamics*

Since the smallest individuals to develop gonadal tissue were 5 mm, gonadal development may begin in year-old seastars based on the rate of growth estimated above. Since oogenesis requires a total of 24 months (Worley, *et al.*, 1977) and mature oocytes appear for the first time in animals no smaller than 15 mm, these sexually mature animals must be about 3 years of age (in their fourth growing season). Therefore, it is likely that the first modal group of seastars (the 9 mm group in Fig. 6) is in its third growing season and the seastars of 15–30 mm (the bulk of the population) and a small number of much larger specimens, may comprise older year classes (Fig. 6). Thus, on the basis of the population size-frequency distribution, we suggest that *L. tenera* lives 4 or more years. Since ripe oocytes are already present in females as small as 15 mm radius (about 3 years old) and gonads are found in individuals as large as 40 mm, *L. tenera* is probably iteroparous.

The growth rate of *L. tenera* is slow compared with broadcasting seastars such as *Asterias* species, but similar to other *Leptasterias* species (Fig. 10). Even *Pisaster ochraceus* (Brandt), a slow-growing broadcast spawner achieves a greater growth rate than *Leptasterias* species, as it attains 22 mm radius in one year (Quayle, 1954).

Menge (1975, p. 96) offers an “. . . interpretive hypothesis that brooding in *L. hexactis* is an evolutionary response to competition-induced small body size.” Specifically, he suggests that brooding in *L. hexactis* is a “coadaptive consequence” of competition with *Pisaster ochraceus*. However, the genus *Leptasterias* is largely composed of cold water (arctic-boreal), slow-growing species (Figs. 9, 10). Thus, it is possible that brooding and associated specializations such as a two-year period of oogenesis (Chia, 1968a, b; Worley, *et al.*, 1977) and a slow rate of growth (Fig. 10) are widespread “cold adaptations” (*sensu* Clarke, 1980) shown by the genus *Leptasterias* rather than the evolutionary consequence of competition in certain species.

There is no evidence that female *L. tenera* suffer greater mortality than males as a consequence of brooding. As inferred from Fig. 7, male mortality exceeds female mortality for sexually mature individuals in the Block Island Sound population. While the behavioral activities associated with spawning may extract some metabolic costs, these have not been measured, nor has the degree and importance of starvation during brooding.

In the winter, we found that feeding activity appeared to be depressed in both male and female *L. tenera*, though our data were few. O'Brien (1976) has suggested that brooding female *L. littoralis* may feed on fine particulate material while brooding. The uptake of dissolved organic materials is also possible, and (though rarely) brooding female *L. hexactis*, *L. pusilla*, and *L. tenera* have been found with ingested prey (Osterud, 1918; Smith, 1971; Menge, 1974; pers. obs.). Moreover, the histological changes which have been interpreted to suggest that female *L. hexactis* cannot feed while brooding are also found in non-brooding species that are capable of feeding throughout the year (Chia, 1969; Nimitz, 1971). Thus, the possible significance of nutrient uptake by brooding female *Leptasterias* invites additional experimentation.

The pyloric caecum index has been used to estimate the energy expenditure involved in brooding (Menge, 1974). However, gametogenesis and maintenance metabolism also draw upon the seastar's energy reserves during the brooding period (Chia, 1968b; Worley, *et al.*, 1977). As Harrold and Pearse (1980) and Lowe and Dearborn (1979) have shown, the allocation of energy from the pyloric caeca is not well enough understood to assume (as suggested by Menge, 1974) that the change in the caecum index before and after brooding approximates the weight an individual loses to gametes and brood handling. Clearly, additional data are required to assess reliably the energetic costs of brooding.

A first approximation of the relative costs of brooding versus broadcast spawning might be developed by comparing the weight of spawned gametes in representative species. The brooding species *L. hexactis* and *L. tenera* lose an estimated 5.5% (Menge, 1974) and 5.6% (this study) of their total body weight during spawning, as compared to from 7–10% and up to 40% in the broadcast spawner *Pisaster ochraceus* (Menge, 1974). We therefore suggest that until accurate calorific budgets are available it should not be assumed that the brooding *Leptasterias* species allocate more energy to reproduction than do broadcast spawning asteroids.

#### ACKNOWLEDGMENTS

We thank Dr. Marie Abbott, Ms. Diane Ashton, Dr. Alan Michael, Mr. Dick Colburn (R/V Asterias, Woods Hole Oceanographic Institution), and Mr. A. A. Campbell and the crew of the R/V UCONN (University of Connecticut) for their assistance with field work, processing of collections, and loan of specimens. We also thank Drs. David L. Pawson, Norman A. Sloan and Paul A. Tyler, Ms. Maureen

Downey, and two anonymous reviewers, whose comments improved the manuscript. To the late Dr. Andrew Norwalk, we are especially grateful for a series of underwater photographs and a generous amount of shiptime.

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